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Inheritance of Resistance to Specific Races of Crown and Stem Rust, to Helminthosporium Blight, and of Certain Agronomic Characters of Oats

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SUMMARY

Observed segregation for reaction to stem rust in several oat crosses was on a monohybrid basis except in the cross Sac x Hajira-Joanette where segregation was observed to be on a three-factor basis. A mesothetic type of reaction to the composite of races 2 and 8 was observed in seedling plants classified as susceptible in two crosses, Mindo x Tama and Sac x Hajira-Joanette. Since no segregation was observed for reaction to race 2 in either of the two crosses, one factor pair for resistance to race 8 must be allelic to the one governing resistance to race 2 possessed by Tama and Hajira x Joanette.

Segregation for reaction to races 1 and 45 of crown rust was on a monogenic, digenic or trigenic basis in different crosses investigated. Five different factors for resistance to crown rust were identified in this study: A and B, complementary dominant factors which give the Bond type (type 0) of resistance of race 1; L, a simple dominant which gives the Landhafer type of resistance (type 0-1) to races 1 and 45; S, a simple dominant from Santa Fe which governs resistance (type 0) to races 1 and 45; and V, a simple dominant of the hypersensitive type (type 2) from Victoria which also governs resistance to races 1 and 45. The factor from Santa Fe (S) appears to be of great promise as a source of resistance to the relatively prevalent race 45. Many desirable agronomic progenies possessing resistance to races 1 and 45 from the cross of Santa Fe x Clinton have been selected for further testing. Very few selections have been made from Mindo x Landhafer for testing in F_4 . The L factor does not appear to be too satisfactory under the conditions of this experiment for resistance in the mature plant stage.

Susceptibility to *Helminthosporium victoriae* was inherited as a simple dominant and completely linked with the hypersensitive type of resistance to *Puccinia coronata avenae* possessed by Victoria. Genetic evidence was presented which suggests that resistance or susceptibility to these two diseases is dependent upon the same factor pair. This relationship would further suggest the inadvisability of utilizing the hypersensitive type of resistance to *P. coronata avenae* of Victoria in attempting to obtain resistance to race 45. The most satisfactory method of salvaging the numerous commercial varieties possessing this type of resistance to crown rust (Vicland, Boone, Cedar, Osage, Tama, etc.) is to remove the V factor and at the same time add such a factor as the one from Santa Fe or Landhafer.

Agreement between seedling and mature plant reaction was generally good for the diseases investigated.

Nodal pubescence, basal hairs and earliness were monogenic in their inheritance, while dwarfness appeared monogenic in one cross and digenic in two others. No linkage was found between these plant and seed characters.

Stem rust reaction and factors governing crown rust resistance were inherited independently of each other and of basal hair numbers, earliness and dwarfness. Reaction to *H. victoriae* was independent of dwarfness and factors A and B for resistance to race 1 of *P. coronata avenae*, but it was completely linked with or governed by the same factor for susceptibility to *H. victoriae*. A strong linkage between pubescent nodes and susceptibility to stem rust was observed in three widely different crosses. A possible linkage of stem rust reaction and reaction to crown rust occurred in the cross of Sac x Hajira-Joanette. It was impossible, however, to determine the nature of this association.

Inheritance of Resistance to Specific Races of Crown and Stem Rust, to Helminthosporium Blight, and of Certain Agronomic Characters of Oats.¹

By S. C. LITZENBERGER²

Crown rust, stem rust and Helminthosporium or Victoria blight have been the most important diseases of oats in this country in recent years. The most satisfactory method of controlling these diseases is by growing resistant varieties. Plant breeders throughout the world are making an effort to develop new biological entities which will give maximum production under their specific environments. Any knowledge that will facilitate the development of superior strains of oats, such as that gained from an inheritance study, should be of value to the plant breeder.

The present study reports the results of experiments on the mode of inheritance of resistance of oats to races 1, 6 and 45 of *Puccinia coronata avenae*, Eriks. & E. Henn.³ (crown rust), races 2, 5, 8 and 10 of *P. graminis*

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The material presented in this bulletin represents a revision of a thesis of a similar title which was submitted by the writer to the Graduate Faculty of Iowa State College in partial fulfillment of the requirements for the degree of doctor of philosophy in March, 1948. A complete copy of the thesis is on file in the Iowa State College Library.

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³According to strict interpretation of the International Rules and Botanical Nomenclature, crown rust and stem rust should be designated *Puccinia coronata* Corda, f. sp. *avenae* (Eriks. & E. Henn.) Eriks., *P. graminis* Pers., f. sp. *avenae* (Eriks. & Henn.) Eriks. respectively; designation of each rust as a special form (forma specialis; f. sp.) is also in accordance with these rules. Because of greater simplicity the names of these two rusts are written as simple trinomials throughout the text.

Reference to races 1 and 6 of *P. coronata avenae* will be as race 1 throughout the paper; races 2 and 5 of *P. graminis avenae* will be as race 2; and races 8 and 10 of *P. graminis avenae* will be as race 8. None of the parental varieties used in this study differentiated these pairs of races; thus there was no attempt to distinguish between them.

avenae Eriks. & E. Henn. (stem rust), and *H. victoriae* Meehan & Murphy (Helminthosporium or Victoria blight) in six different oat crosses. Records were also taken and reported on certain morphological characteristics such as dwarfness, earliness, number of basal hairs and nodal pubescence for determining possible linkage relationships.

REVIEW OF LITERATURE

REACTION TO STEM RUST

Inheritance of resistance to *Puccinia graminis avenae* was first reported by Garber (12, 13)⁴ who studied progenies of crosses of White Russian (White Tartar), a resistant variety, with two susceptible varieties, Minota and Victory. He found that resistance to stem rust was inherited as a single dominant factor. Since this early report others (3, 7, 17, 18, 19, 21, 36, 40, 43, 45) have reported similar results regardless of whether or not they used composite inoculum or individual races. A single recessive gene for resistance was reported by Dietz (7) in a cross of White Russian with a selection from Burt while two factors, one operating as an inhibitor and the other as a dominant for resistance, were necessary to explain his results when he studied progenies of another strain of Burt oats crossed with White Russian. Reaction of seedlings was consistent with adult plant reaction in all of the studies reviewed. Also, the reaction to stem rust was inherited independently of such characters as lemma color, length, strength or presence of awns, basal articulation, number and length of basal hairs, culm diameter, breaking strength of straw, panicle type, maturity, shattering and reaction to loose and covered smut, blast and crown rust.

The inherent resistance of the principal varieties of oats to 12 races of *P. graminis avenae* has been summarized by Levine and Smith (22) and Newton, et al. (31) who have classified oat varieties into six major groups typified by the varieties White Tartar (Group I, resistant to races 1, 2, 5, 8, 9 and 10), Hajira x Joannette and Garry (Group II and III, respectively, resistant to all 12 races), Richland (Group IV, resistant to races 1, 2, 3, 5, 7 and 12), Joannette strain (Group V, resistant to races 1, 3 and 4), and Bond (Group VI, not resistant to any of the 12 races). Resistance to all known races of *P. graminis avenae* is now

⁴Reference by number is to Literature Cited, page 494.

available for incorporation into varieties of desirable agronomic type. This includes resistance to the newly reported race 14 isolated from *Poa ampla* Merr. by Fischer and Claassen (9).

REACTION TO CROWN RUST

The inheritance of resistance to *P. coronata avenae* is much more complex than the inheritance of resistance to *P. graminis avenae*. Factorial analysis necessary for interpreting results obtained with different crosses investigated range from a simple dominant factor for resistance (3, 4, 5, 8, 19, 28, 30, 44) to a multiple factor hypothesis with susceptibility partially dominant (33).

Various two-factor differences for resistance have been reported by numerous workers. Dietz and Murphy (8) found in addition to a factor pair governing resistance, an inhibitor gene which resulted in an F_2 segregation of 13 susceptible to 3 resistant. Similarly, Torrie (40) and Ko, et al. (21) report the presence of a partial inhibitor gene which masks crown rust resistance. This results in a modified complementary interaction. Two dominant complementary factors were found by Hayes, et al. (19), Weetman (44), and Ko, et al. (21), while four factor pairs, two sets of dominant complementary factors, explained the results of Cochran, et al. (3). One set of these complementary genes governed resistance, while the other set acted as dominant complementary inhibitor genes which were epistatic to the genes for resistance.

Resistance of Bond to race 1 is distinct from that of Victoria (3, 44) which imparts resistance to races 1 and 45. The resistance of Bond which approaches immunity is conditioned by two dominant complementary genes, while Victoria type of resistance is dependent upon one dominant factor. Smith (36) was unable to recover the number of susceptible types expected on a single factor basis in crosses of Victoria with Minrus, Anthony, and the Double Cross II-22-220.

In correlated inheritance studies (19, 36, 40) all characters studied in relation to crown rust were inherited independently of each other. An apparent complete linkage between resistance to crown rust and susceptibility to *Helminthosporium victoriae* was reported by Murphy and Meehan (28). Association between seedling and mature plant reaction to crown rust was strong (3, 19, 36, 40).

The number of races of *P. coronata avenae* is great and largely depends upon the number of differential varieties used. On the basis of unpublished data on 13 differential varieties, Murphy (26) has reported 87 known races as occurring in North America. Straib (39) using 15 differential varieties isolated 142 races in Europe, while Vallega (41) described 4 races in Argentina with 13 standard varieties. Bond is highly resistant to 79 of the 87 races reported by Murphy (26). Of the races to which Bond is susceptible, only race 45 has become sufficiently prevalent in the United States in recent years to threaten the continued good performance of newer varieties such as Clinton, Benton, Mindo, Bonda and others (1, 34). Victoria is resistant to 83 of the 87 reported races of crown rust (26). None of the races which attack Victoria is prevalent in the United States, but the use of the hyper-sensitive type of resistance is limited because of the association of it with susceptibility to *H. victoriae*.

REACTION TO *HELMINTHOSPORIUM VICTORIAE*

Reaction in the F_2 to *H. victoriae* was according to a single factor difference with susceptibility completely dominant in eight crosses studied by Murphy and Meehan (28). Field and greenhouse varietal reactions were not different. A complete linkage for genes governing resistance of the Victoria type to crown rust and susceptibility to *H. victoriae* was suggested from the results obtained.

CHARACTERS OTHER THAN REACTION TO DISEASE

Dwarf oats found in a head row of Victory were reported by Warburton (42) to contain a single gene inherited as a simple recessive while a simple dominant gene was found by Stanton (37) to control dwarfness in segregates from Aurora x Pringle Progress and Winter Turf x Sixty-Day, all normally tall oat varieties. It was not possible to interpret inheritance of dwarfness on a factorial basis in the study by Goulden (16).

Evidence of a single factor (6, 35), two factors (14, 40), three factors (2), and multiple factors (6, 32, 35, 40) governing earliness has been variously reported in different crosses investigated. Partial dominance of earliness has been reported by several investigators (14, 32, 35, 40). Earliness was found inherited independently of crown

and stem rust reaction in one cross involving Bond (40). The number or length of basal hairs was found by most workers (11, 19, 35, 36, 40) to be dependent upon one factor pair with shortness or no (or few) basal hairs dominant. Only Shaw and Bose (35) reported a di-hybrid ratio for basal hair number. Other than the linkage relationship with other seed characters, such as spikelet disarticulation, hairy rachilla, floret disjunction and awning, basal hairs have been reported inherited independently. This includes reaction to the rusts.

No inheritance studies have been found which report the presence or absence of nodal pubescence in oats.

MATERIALS

Six oat crosses were selected for this study from a number of crosses which had been made in the greenhouse at Ames, Iowa, during the winter of 1944-45 as part of the cooperative oat improvement program at the Iowa Agricultural Experiment Station. Reaction to specific races of *Puccinia graminis avenae*, *P. coronata avenae* and *Helminthosporium victoriae*, together with a brief description of characters investigated for the parents of the different crosses, are presented in table 1 and illustrated in figs. 1 and 2. All parental varieties belong to the species *Avena sativa* L., except Bond and Landhafer, which belong to *A. byzantina* C. Koch. Victoria, Santa Fe and Landhafer are introductions from South America. Bond, an Australian introduction, was selected from *A. sterilis* x Golden Rain. D67, Tama, Clinton and Sac were developed cooperatively by the Iowa Agricultural Experiment Station and the United States Department of Agriculture. D67 is a selection from Richland x Green Russian. Tama is a Victoria x Richland selection which possesses the crown rust resistance of the Victoria parent. Clinton and Sac were selected from the cross of D69 (Richland x Green Russian) by Bond. The Minnesota Agricultural Experiment Station selected Mindo from a cross of Bond x (Minota-White Russian x Black Mesdag). Hajira x Joannette was selected in Canada by Welsh (46) as being resistant to all known races of stem rust.

Subsequent increases and collections of races 1 and 45 of *P. coronata avenae* and races 2 and 8 of *P. graminis avenae* were made on the following varieties: Iogold (*P. coronata avenae*, race 1), Clinton (*P. coronata avenae*,

TABLE 1. REACTION OF PARENT LINES TO DIFFERENT RACES OF *PUCCINIA GRAMINIS AVENAE*, *P. CORONATA AVENAE* and *HELMINTHOSPORIUM VICTORIAE*, TOGETHER WITH PLANT AND SEED CHARACTERS OF PARENTS.

Variety and cross	C. I. no.	Reaction of parent lines*					Contrasting plant and seed characters studied		
		<i>P. graminis avenae</i>		<i>P. coronata avenae</i>		<i>H. victoriae</i>	Nodal pubescence	Dwarfiness	No. of basal hairs
		Races 2, 5	Races 8, 10	Races 1, 6	Race 45				
Bond Victoria	2733 2401	S(4) S(4)	S(4) S(4)	R(0) R(2)	S(4) R(2)	R S			
Mindo Tama	4328 3502	R(2) R(2)	R(2) S(4)	R(0) R(2)	S(4) R(2)	R S		Normal Normal	
D67 Bond	2870 2733	R(2) S(4)	R(2) S(4)	S(4) R(0)	S(4) S(4)	R R	Absent Present	Normal Normal	None Numerous
Mindo Landhafer	4328 3522	R(2) S(4)	R(2) S(4)	R(0) R(0)	S(4) R(0)	R R	Absent Present	Normal Normal	None Numerous
Santa Fe Clinton	4518 3971	S(4) R(2)	S(4) R(2)	R(0) R(0)	R(0) S(4)	R R	Present Absent		
Sac Hajira x Joannette	3907 4023	R(2) R(1)	R(2) R(1)	R(0) S(4)	S(4) S(4)	R R		Normal Normal	

*Reaction of host to pathogen; R, resistant; S, susceptible. Numbers in parenthesis refer to infection type; 0, nearly immune; 1, highly resistant; 2, moderately resistant; 3, moderately susceptible; 4, completely susceptible.

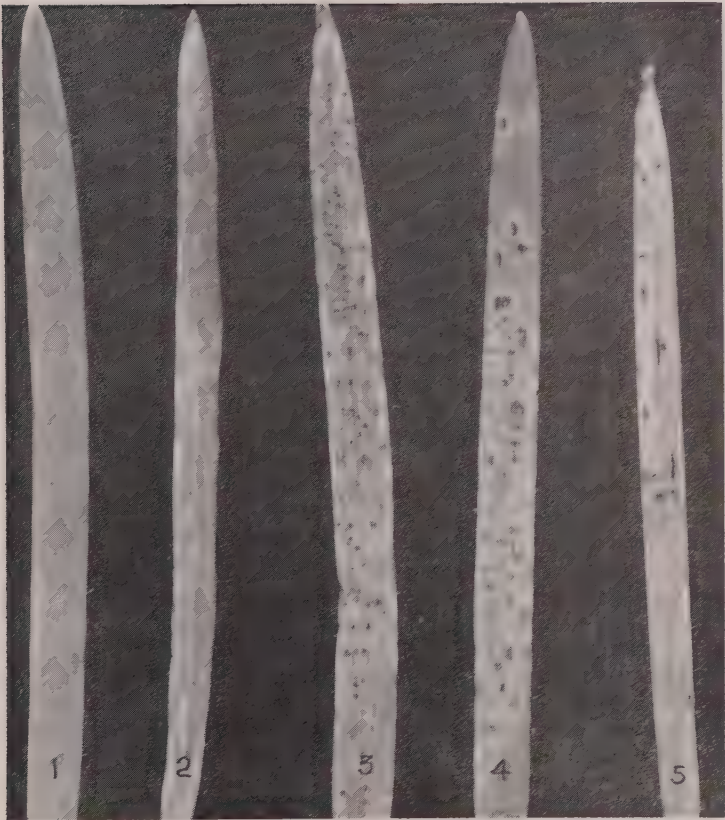


Fig. 1. Seedling reaction to *Puccinia graminis avenae*: (1), uninoculated check; (2), highly resistant or type 1 of Hajira x Joannette; (3) moderately resistant or type 2 of Clinton, D67, Minto, Sac and Tama (race 2); (4) highly susceptible or type 4 of Bond, Victoria and Tama (race 8); and (5) mesothetic or type x of a Sac x Hajira-Joannette segregate.

race 45), Landhafer (*P. graminis avenae*, race 2), and Boone (*P. graminis avenae*, race 8). *Helminthosporium victoriae* was cultured as suggested by Litzenberger and Murphy (23).

EXPERIMENTAL METHODS

FIELD STUDIES

F₂ and F₃ generations of all crosses investigated were grown in 1946 and 1947 at Ames, Iowa. About a hundred

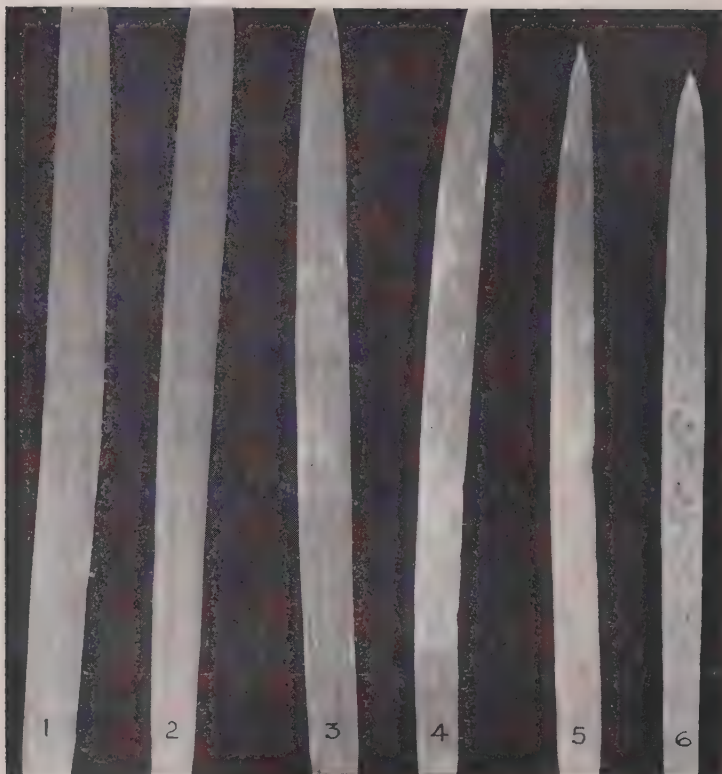


Fig. 2. Seedling reaction to *Puccinia coronata avenae*: (1) uninoculated check; nearly immune or type 0 of (2) Bond, Clinton, Mindo and Sac, (3) Landhafer and (4) Santa Fe; moderately resistant or type 2 of (5) Victoria and Tama; and (6) highly susceptible or type 4 of D67 and Hajira $\times$ Joannette and of Bond, Clinton, Mindo and Sac to race 45.

F_2 seeds of each cross were space-planted 4 inches apart in rod rows with the parental varieties in the two adjacent rows. Five such seedlings were made at isolated locations so that epiphytotics of each race of *Puccinia graminis avenae*, *P. coronata avenae* and *Helminthosporium victoriae* could be made possible for each cross included in the study. Several rows of susceptible hosts, the same varieties as those listed for greenhouse increase, were seeded around each nursery. The susceptible F_2 plants in the different nurseries were tagged and at harvest time the plants were pulled, brought to the laboratory and threshed individually

so that the F_3 breeding behavior of each F_2 plant could be studied.

F_3 progenies with sufficient seed for testing were planted in 1947 in 4-foot rows with approximately 35 seeds per row. The number of lines of each cross planted ranged from 347 to 486, mortality being high in some crosses. A composite of various races of *P. graminis avenae* and *P. coronata avenae* was used as inoculum in the field during 1947.

Classifications of F_2 and F_3 plants also were made for dwarfness, nodal pubescence, number of basal hairs on the lower floret, and earliness. Different classes recognized for these physical characters are similar to those reported by other workers who have studied their mode of inheritance. They are as follows: for dwarfness, normal and dwarf; basal hairs, numerous and absent; nodal pubescence, pubescent and nonpubescent; and earliness, early and late.

Epiphytotics of stem rust and crown rust were most effectively produced by hypodermically injecting a suspension of uredospores into culms of the susceptible seedling plants grown in border rows in the nursery. Inoculations were continued until an epiphytotic prevailed in the susceptible borders. Uredospores also were dusted over the entire nurseries during several evenings following rain, but this method was relatively ineffective in establishing epiphytotics. There was adequate rust infection for proper classification of the material each season.

During 1946 *H. victoriae* was sprayed as a mycelial suspension on seedlings during late evening following a rain. Approximately 50 milliliters of "basic" mycelial suspension, prepared according to the method described by Litzenberger and Murphy (23) was applied with an ordinary hand sprayer to 100 plants. Such a treatment did not kill the susceptible plants before some seed was produced. Susceptible plants could be readily distinguished from resistant ones, as noted by Meehan and Murphy (24), by premature ripening, blackened nodes and broken-over culms near the ground line. A few days following application of the mycelial suspension the lower leaves of susceptible plants became reddish-orange.

GREENHOUSE STUDIES

F_2 and F_3 generations of the several crosses investigated were grown in the greenhouse in 1946 and 1947. Only F_2 progenies from the cross of Bond x Victoria were studied

during 1946. Approximately 300 F_2 plants from each cross were grown. When individual plants were studied for reaction to different races of rust, the first leaf was inoculated with race 1 or 45 of *P. coronata avenae*, and after readings were completed, the leaf was removed and the second leaf was inoculated with a composite of races 2 and 8 of *P. graminis avenae*. Following the recording of the reaction to stem rust, a third inoculation was made on another blade of these same plants with the second race of crown rust.

Spores were applied to the leaf surface of individual plants with a flat needle using the method described by Murphy (27). When F_2 plants and their F_3 progenies were inoculated with only a single race, spores were applied by dusting with a mixture of 1 part spores to about 50 parts talc. After dusting the plants were placed in a moist chamber for 24 hours and then removed to the greenhouse bench for incubation. This method proved very effective in obtaining uniform infection. Rust readings were made about 10 days after inoculation. Seedlings were classified according to their rust reaction using the infection types described by Murphy (27) and Levine and Smith (22). Infection types 0, 1 and 2 were classified as resistant, while types 3 and 4 were classified as susceptible.

To determine the reaction to *H. victoriae* in the greenhouse, the method described by Litzenberger and Murphy (23) was employed. Seedling plants were sprayed with a 5 percent dilution of the unscraped basic mycelial suspension and placed in a moist chamber for at least 36 hours before removal to the greenhouse bench. Only two classes of reaction, resistant or susceptible, were recognized following inoculation with *H. victoriae*. Susceptible plants died while resistant ones were unaffected.

For character studies in the greenhouse other than disease resistance, F_2 plant progenies were classified according to classes given in the previous section. For most reports of inheritance of characters, other than reaction to disease, only F_3 data are listed.

STATISTICAL ANALYSIS OF DATA

The chi-square test was used for determining goodness of fit of observed data with those expected and for association of specific characters.

Linkage intensities were estimated from F_3 data by the method of maximum likelihood described by Immer (20) and later simplified by Stevens (38).

EXPERIMENTAL RESULTS

INHERITANCE OF REACTION TO STEM RUST

Seedling and mature plant reactions to races 2 and 8 of *Puccinia graminis avenae* were investigated in six different oat crosses: Bond x Victoria, Mindo x Landhafer, D67 x Bond, Santa Fe x Clinton, Mindo x Tama, and Sac x Hajira-Joanette. The reaction of seedling plants to specific races was determined in the greenhouse, while reaction of mature plants to artificially induced epiphytotics was obtained in the field during 1946 and 1947. The reaction of F_2 plants to separate races was obtained in the field, while reaction of the F_3 lines was obtained only to a composite of the two races. In the greenhouse a composite of races 2 and 8 was used for determining the reaction of F_2 and F_3 generations.

Segregation for reaction to stem rust under field and greenhouse conditions and tests for goodness of fit are presented in table 2. Studies on inheritance of stem rust resistance are reported under three major parental headings.

CROSSES OF SUSCEPTIBLE VARIETIES

In a single planting in the greenhouse, no segregation was observed for resistance in the seedling stage to a composite of races 2 and 8 among 114 F_2 plants of the cross of two susceptible varieties, Bond x Victoria. Uredia on the progeny were like those on the susceptible parents, type 4 or highly susceptible. This is as expected, since neither variety possesses known genes for resistance to these races of stem rust.

CROSSES OF RESISTANT AND SUSCEPTIBLE VARIETIES

Progenies of four crosses each involving resistant and susceptible parents were studied in the greenhouse and field for reaction to races 2 and 8 of stem rust. The crosses Mindo x Landhafer, D67 x Bond, and Santa Fe x Clinton, each have one susceptible parent, while in the Mindo x

TABLE 2. INHERITANCE OF RESISTANCE TO RACES 2 AND 8 OF *Puccinia graminis avenae* IN SEVERAL OAT CROSSES GROWN IN THE FIELD AND GREENHOUSE.

Varietal combination and location of epiphytotic	Inoculum (races)	Generation	Observed or expected*	No. of plants or lines		Chl.-square	P
				Res.	Seg.		
Crosses of susceptibles Bond x Victoria Greenhouse Crosses of resistant and susceptibles Mindó x Landhafer Field	2,8	F ₂	O E		114 114	0.0	1.0
	2	F ₂	O E	53 52.5	17 17.5	0.02	0.9-0.8
	8	F ₂	O E	55 50.3	12 16.8	1.8	0.2-0.1
	2,8	F ₃	O E	85 86.8	76 173.5	2.3	0.4-0.3
Greenhouse	2,8	F ₂ **	O E	224 231	84 77	0.9	0.4-0.3
Mindó x Tama Field Field Greenhouse	8	F ₂	O E	60 60	20 20	0.0	1.0
	2,8	F ₃	O E	91 93.5	85 93.5	1.5	0.5-0.4
	2,8	F ₂ **	O E	227 232.5	83 77.5	0.5	0.5-0.4
	2	F ₂	O E	71 66.8	18 22.3	1.1	0.3-0.2
Crosses of resistant and susceptibles D67 x Bond Field	8	F ₂	O E	64 62.3	19 20.8	0.2	0.7-0.8
Field	2,8	F ₃	O E	119 109.8	107 109.8	1.0	0.7-0.6

each have one susceptible parent, while in 3

TABLE 2 (Continued)

Varietal combination and location of epiphytotic (Continued)	Inoculum (races)	Generation	Observed or expected*	No. of plants or lines		Chi-square	P
				Res.	Seg.		
Crosses of resistant and susceptibles							
Greenhouse	2,8	F ₂	O E	234 247.5		3.0	0.1-0.05
Santa Fe x Clinton							
Field	2	F ₂	O E	56 56.3		0.01	1.0-0.9
Field	8	F ₂	O E	66 68.3		0.3	0.9-0.8
Field	2,8	F ₂	O E	101 103	213 206	0.5	0.8-0.7
Greenhouse	2,8	F ₂	O E	211 214.5		0.2	0.7-0.6
Crosses of resistant							
Mindo x Tama	2	F ₂	O E	76 76		0.0	1.0
Sac x Hajira-Joanette							
Field	2	F ₂	O E	86 86		0.0	1.0
Field	8	F ₂	O E	100 102.4		3.5	0.1-0.05
Field	2,8	F ₂	O E	286 281	188 197.4	3.1	0.3-0.2
Greenhouse	2,8		O E	354 355.4	7 5.6	0.3	0.6-0.5

*In the crosses where segregation occurred for reaction to stem rust chi-square was calculated on the expected ratio of 3:1 or 1:2:1 as the case required, except in the cross of Sac x Hajira-Joanette, where the expected was 63:1 or 37:26:1.

**Calculations based on corrected F₂, since a few F₃ plants were misclassified.

Tama cross, Mindo is resistant to races 2 and 8 and Tama is resistant only to race 2.

Segregation for stem-rust reaction gave a good fit to the 3:1 or 1:2:1 ratio expected in the F_2 or F_3 , respectively, on a monogenic basis, both in seedling and mature-plant stages (table 2). All P values fell between 1.0 and 0.1. Evidently a single dominant gene was responsible for resistance to races 2 and 8 in the varieties Mindo, D67 and Clinton. Since Tama and Mindo are genetically different, as evidenced by their differential reaction to race 8 and the lack of occurrence of progenies susceptible to race 2 in the F_2 or F_3 , it would be logical to assume that the genes of Tama for resistance to race 2 and those for resistance to races 2 and 8 of Mindo form an allelic series. In any one cross, as was observed in the case of Mindo x Tama, the only homozygous types that could be obtained are parental types, i. e., those resistant to race 2 or those susceptible to race 8 or a composite of the two races.

CROSSES OF RESISTANT VARIETIES

Varying results were obtained with crosses of resistant varieties (table 2). In the cross of Mindo x Tama no segregation for reaction to race 2 was observed. All progenies are resistant (type 2) to this race. However, as noted in the previous section, segregation occurred for reaction to race 8 on a single factor basis with resistance dominant. Therefore, the factor pair governing resistance to race 2 of Tama must be allelic to the factor pair of Mindo that governs resistance not only to race 2, but to race 8 as well. Thus, one would expect, as was observed, no segregation for reaction to race 2, but segregation on a monohybrid basis for race 8. This was phenotypically obvious in progenies inoculated with a composite of the two races. Plants susceptible to a composite of races were actually susceptible to race 8, but not to race 2. The plants thus exhibited a mesothetic reaction, i. e., race 8 pustules continued to develop into a 4-type reaction, while race 2 did not develop beyond the 2-type stage. Under field conditions the mesothetic reaction was not apparent because of the masking action of race 8 on susceptible hosts.

The segregation pattern in the cross of the two resistant varieties, Sac x Hajira-Joanette, was similar to that observed in the Mindo x Tama cross. Both parents were resistant to races 2 and 8, but plants exhibiting a mesothe-

tic reaction to a composite of these races occurred among the F_2 and F_3 progenies. Plants with a mesothetic seedling reaction (types 2 and 4) appeared to be susceptible (type 4) as they became older. Under field conditions plants which might have given an early mesothetic reaction also gave a susceptible reaction (type 4).

Since plants classified as mesothetic later appeared susceptible both in seedling and mature plant stages, and those plants classified as resistant (types 1 and 2) remained resistant, separating the progenies into two classes (resistant or susceptible) was considered sound. As can be seen in table 2, occurrence of these susceptible types was on a three-factor basis with resistance dominant in the seedling and mature plant stages when source of inoculum was either race 8 or a composite of races 2 and 8. In the field four F_2 plants in a population of 104 were susceptible to race 8, and in an F_3 population on this same cross, 12 lines out of 486 were susceptible to a composite of races 2 and 8, 286 were resistant and 188 segregated variously for resistance and susceptibility. In another population investigated in the greenhouse 7 out of 361 plants were susceptible to the composite inoculum of the two races. No segregation for resistance to race 2 was observed under field conditions or in the greenhouse. All plants susceptible to the composite inoculum and race 8 were individually checked and found to be resistant to race 2. P values for the three populations studied with respect to reaction to race 8 and a composite of races 2 and 8 were between 0.6 and 0.05, which indicated that the observed segregations did not deviate significantly from the expected trigenic ratio, with resistance dominant.

Although observed segregation was on a three-factor pair basis, four different factors for resistance to races 2 and 8 were apparently involved in the cross of Sac x Hajira-Joanette. Two were allelic and behaved in a manner similar to that described in the Mindo x Tama cross. This resulted in no segregation for susceptibility to race 2, but there was segregation for susceptibility to race 8 on a monohybrid basis at this locus. It can be assumed from other studies that Sac carries the factor governing resistance to races 2 and 8 and Hajira x Joanette possesses the allele for resistance to race 2. The other two factor pairs which give resistance to race 8 would have to be carried by Hajira x Joanette in the dominant condition. Thus, in crosses there would be segregation on a three-factor basis

TABLE 3. INHERITANCE OF RESISTANCE TO RACE 45 OF *PUCCINIA CORONATA* AVERAGE IN SEVERAL OAT CROSSES GROWN IN THE FIELD AND GREENHOUSE.

Varietal combination and location of epiphytotic	Gener- ation	Observed or expected*	No. of plants or lines			Chi- square	P
			Res.	Seg. or Int.	Susc.		
Crosses of susceptible D67 x Bond Field	F ₂	O			93	0.0	1.0
Field	F ₂	E			93		
Greenhouse	F ₂	O			439	0.0	1.0
	F ₂	E			439		
	F ₂	O			330	0.0	1.0
	F ₂	E			330		
Sac x Hajira-Joanette Field	F ₂	O			103	0.0	1.0
Field	F ₂	E			103		
Greenhouse	F ₂	O			486	0.0	1.0
	F ₂	E			486		
	F ₂	O			361	0.0	1.0
	F ₂	E			361		
Crosses of resistant and susceptible Bond x Victoria Greenhouse	F ₂	O	82		32	0.6	0.5-0.4
	F ₂	E	85.5		28.5		
Mindo x Tama Field	F ₂	O	63		19	0.2	0.7-0.6
Field	F ₂	E	61.5		20.5		
Greenhouse	F ₂	O	82	183	109	4.1	0.2-0.1
	F ₂ **	E	93.5	187	93.5		
	F ₂ **	O	229		85	0.7	0.5-0.4
	F ₂ **	E	235.5		78.5		
Mindo x Landhafer Field	F ₂	O	45		27	6.0	< 0.05
Greenhouse	F ₂	E	54		18		
Greenhouse	F ₂	O	79		91	1.1	0.6-0.5
Greenhouse	F ₂ **	E	87.3	179	87.3		
	F ₂ **	O	377	174.5	116	0.6	0.5-0.4
	F ₂ **	E	369.8		123.3		
Santa Fe x Clinton Field	F ₂	O	60		26	1.3	0.3-0.2
Field	F ₂	E	64.5		21.5		
Greenhouse	F ₂	O	101	213	98	0.5	0.8-0.7
	F ₂	E	103	206	103		
	F ₂	O	73	141	72	0.1	0.9-0.8
	F ₂	E	71.5	143	71.5		

*Expected ratios in F₂ plants or lines were on the basis of 3:1 or 1:2:1, respectively.**Observed numbers are on a partially corrected F₃ basis.

for reaction to race 8 and to a composite inoculum of 2 and 8, while all progenies would be resistant to race 2.

Some of the segregating lines exhibited increased resistance to races 2 and 8 of *P. graminis avenae* beyond that of either parent, since types were observed which approached an 0 type reaction. Selections from this cross might serve as an excellent reservoir of germ plasm for increased resistance to stem rust.

INHERITANCE OF REACTION TO CROWN RUST

Reaction of seedling and mature plants to races 1 and 45 of *P. coronata avenae* was investigated in the same six crosses studied for reaction to *P. graminis avenae*. Mature plant reactions were recorded in the field during 1946 and 1947, while seedling observations were made in the greenhouse. Since inheritance of reaction to race 45 and to race 1 is quite different, the results are reported separately.

INVESTIGATIONS WITH RACE 45

CROSSES OF SUSCEPTIBLE VARIETIES

As shown in table 3, no segregation was observed for reaction to race 45 in different groups of F_2 and F_3 progenies of D67 x Bond and Sac x Hajira-Joanette. All segregates were as susceptible (type 4) to race 45 as their parents in the seedling and mature stages.

CROSSES OF RESISTANT AND SUSCEPTIBLE VARIETIES

Progenies of Bond x Victoria, Mindo x Tama, Mindo x Landhafer and Santa Fe x Clinton were studied in the F_2 and F_3 for reaction to race 45 of crown rust. Victoria and Tama possess a hypersensitive type of resistance (type 2) to race 45, while Landhafer and Santa Fe have one of near immunity (type 0). As shown in table 3, segregation for reaction to race 45 in the F_2 and F_3 was very similar for the four crosses. This was evidenced by occurrence of resistant and susceptible plants in the F_2 and F_3 in the ratio of 3 resistant to 1 susceptible or F_3 lines breeding in the ratio of 1 resistant: 2 segregating: 1 susceptible. The observed and expected segregation on a single factor difference was very close, as indicated by relatively high P values. Only in one group of 72 F_2 progenies of the

Mindo x Landhafer cross in the field was there a comparatively poor fit to the expected ratio of 3 resistant to 1 susceptible ($P=0.02-0.01$). Eighteen was the expected and 27 the observed number of susceptible plants in this small population. This slight discrepancy may be the result of a poor sample.

Although resistance to race 45 was inherited on a single factor difference in the four crosses, the factors for resistance to crown rust carried by Landhafer, Santa Fe and Victoria or Tama may not be the same. The Victoria gene (V) for resistance to race 45 probably is different from the others because of its distinct type reaction. Resistance is apparently the result of destruction of host cells around the infection locus. As a result the obligate parasite's development is terminated, and the host is in effect resistant. Victoria type of resistance to *P. coronata avenae* affords adequate host protection under field conditions.

Santa Fe and Landhafer in the seedling stage are similar in their reaction to race 45. Each gives a type 0 reaction, i. e., chlorotic flecks occur on the leaves at points of infection. With both varieties heterozygous progenies resulting from crosses with susceptible varieties exhibit an incomplete dominance of resistance. The completeness of the expression of the dominant gene seems to be influenced by external environment and age in both cases, but in Landhafer it is more easily influenced than in Santa Fe. As plants become older, penetrance of the Landhafer gene for resistance becomes less, and infected heterozygous plants may reach the classification of moderately susceptible (type 3). Since the two varieties belong to two different species and inheritance for resistance to race 1 is different, as is mature plant reaction, it is assumed that the factors for resistance of Santa Fe and Landhafer are probably dependent upon different genetic factors. The Santa Fe factor is designated as S and the Landhafer factor as L for convenience of identification of genes governing resistance to crown rust.

INVESTIGATIONS WITH RACE 1

CROSSES OF RESISTANT AND SUSCEPTIBLE VARIETIES

In the crosses D67 x Bond and Sac x Hajira-Joanette, each contained one resistant parent of similar reaction to race 1 (type 0), while D67 and Hajira x Joanette were

completely susceptible (type 4). Mature plant reactions of the F_2 generation in the field in 1946 and seedling reactions of F_2 and F_3 generations in the greenhouse in 1946 and 1947, respectively, are summarized in table 4. Both crosses segregated for reaction to race 1 in the mature plant and seedling stage. The F_2 generation segregated on the basis of 9 resistant plants to 7 susceptible, while the F_3 lines bred 1 resistant to 8 segregating to 7 susceptible. Comparing individual results obtained in table 4 with ratios expected, P values of between 0.9 and 0.1 were obtained except in the single case of observations made in the field with a relatively small F_2 population of Sac x Hajira-Joanette. The expected on a basis of 9 resistant to 7 susceptible plants was 55.7 and 43.3, and the actual number observed was 67 and 32, respectively. The fairly low P value of between 0.05 and 0.02 obtained in this particular case probably is due to chance sampling.

Inheritance of resistance to race 1 of crown rust in these two crosses can be explained on a two-factor difference. Two dominant complementary factors (A and B) are carried by Bond and Sac parents. Both factors are inherited independently and both must be present to give a plant the expression of the Bond type of resistance. If either or both of these factors are recessive (aaBB, aaBb, AAbb, Aabb or aabb) the plant is completely susceptible and will breed true for susceptibility.

CROSSES OF RESISTANT VARIETIES

F_2 and F_3 progenies of four crosses (Santa Fe x Clinton, Bond x Victoria, Mindo x Tama and Mindo x Landhafer) were studied in which segregation occurred for reaction to race 1 of *P. coronata avenae* even though all parents were resistant. Clinton, Mindo and Bond are nearly immune, with a reaction type 0. The reactions of Landhafer and Santa Fe are similar, but differ from the Bond type of reaction to race 1 in that more chlorotic flecking develops following inoculation. Victoria and Tama have a type 2 reaction.

As shown in table 4, susceptible plants occurred in F_2 in the ratio of 1 to 15 in the cross of Santa Fe x Clinton and 7 to 57 in the other three crosses in both field and greenhouse studies. In F_3 all susceptible plants bred true while resistant plants either bred true or segregated for susceptibility and resistance. Agreement between observed and expected counts generally was good.

TABLE 4. INHERITANCE OF RESISTANCE TO RACE 1 OF *PUCCINIA CORONATA* AVENAE IN SEVERAL OAT CROSSES GROWN IN THE FIELD AND GREENHOUSE.

Varietal combination and location of epiphytotic crosses of resistant and susceptibles	Generation	Observed or expected*	No. of plants or lines			Chi-square	P
			Res.	Seg. or int.	Succ.		
D67 x Bond Field	F ₂	O E(9:7)	49 50.1		40	0.05	0.9-0.8
Greenhouse	F ₃	O	29	224	186	0.4	0.9-0.8
Greenhouse	F ₂	E(1:8.7)	27.4	219.5	192.1	0.9	0.4-0.3
		O	177		153		
		E(9:7)	185.6		144.4		
Sac x Hajira-Joanette Field	F ₂	O	67		32	5.3	<0.05
Greenhouse	F ₃	E(9:7)	55.7		43.3	2.1	0.4-0.3
Greenhouse	F ₂	O	28	259	199	1.9	0.2-0.1
		E(1:8.7)	30.4	243	212.6		
		O	216		145		
		E(9:7)	203.1		157.9		
Crosses of resistant Santa Fe x Clinton Field	F ₂	O	71		2	1.5	0.3-0.2
Greenhouse	F ₃	E(15:1)	68.4		4.6	2.5	0.3-0.2
Greenhouse	F ₂	O	165	222	24	0.6	0.5-0.4
		E(7:8.1)	180.3	206	25.8		
		O	285		21		
		E(15:1)	268.1		17.9		
Bond x Victoria Greenhouse	F ₂	O	163		29	3.4	0.1-0.05
		E(57:7)	171		31		
Mindo x Tama Field	F ₂	O	54		12	3.6	0.1-0.05
Greenhouse	F ₃	E(57:7)	58.8		7.2	2.4	0.2-0.1
Greenhouse	F ₂ **	O	98	232	45	0.6	0.5-0.4
		E(19:38:7)	111.3	222.7	41.0		
		O	284		30		
		E(57:7)	279.7		34.3		
Mindo x Landhafer Field	F ₂	O	66		8	<0.01	1.0-0.9
Greenhouse	F ₃	E(57:7)	65.9		8.1	3.0	0.3-0.2
Greenhouse	F ₂ **	O	108	212	28	0.8	0.4-0.3
		E(19:38:7)	103.3	206.6	38.1		
		O	154		23		
		E(57:7)	157.6		19.4		

*O is observed count and E is expected.

** Observed count is on a partially corrected F₃ basis.

In the cross of Santa Fe x Clinton two dominant independently inherited factors apparently govern resistance to race 1, since the susceptible types occurred in the ratio of 1 to 15 in F_2 under field and greenhouse conditions, while F_3 lines segregated 7 resistant to 8 segregating to 1 susceptible. Expected numbers for a 15:1 or 7:8:1 phenotypic ratio were very close to those observed for all populations studied, the P values being between 0.5 and 0.2.

Since Clinton possesses the Bond type of reaction to race 1 and is of Bond parentage it is assumed that Clinton carries two dominant complementary factors (A and B) for resistance to race 1 of *P. coronata avenae* as was found for Sac and Bond. It also is known from inoculation studies that the factor for resistance to crown rust of Santa Fe is governed by a single dominant factor (S) which also gives resistance to race 45. (See section on investigations with race 45.) Thus with three known factors present in these two varieties for crown rust resistance (A and B from Bond and S from Santa Fe) and segregation occurring for only two factor pairs, A or B must be common to each of the two parents. This would account for segregation occurring on a dihybrid basis with genes S and A or B contributing equally toward resistance to race 1 in this cross. These assumptions were verified when breeding behavior of F_2 plants and lines was determined for separate reactions to race 1 or race 45. Observed and expected counts with 412 F_3 lines when inoculated with separate races and the breeding behavior obtained are given in table 5. Observed and expected frequencies were in good agreement.

Inheritance of resistance to race 1 in the cross of Mindo x Landhafer was governed by interaction of two dominant complementary factors from Mindo (A and B) with the simple dominant (L) carried by Landhafer. As shown in table 4, susceptible plants occurred in F_2 in the ratio of 7 in 64 in both field and greenhouse studies, and in F_3 these susceptible plants bred true. Resistant plants in the F_3 generation either bred true for resistance or segregated for resistance and susceptibility as expected on a three-factor basis with A and B dominant complementary factors and L a simple dominant for resistance to race 1. Observed counts were in good agreement with expected.

F_2 and F_3 segregation in crosses of Bond x Victoria and Mindo x Tama was similar (table 4). In two F_2 populations studied in the field and greenhouse, resistant plants

TABLE 5. FACTORIAL ANALYSIS* AND BREEDING BEHAVIOR IN F_3 OF SANTA FE x CLINTON TO INDIVIDUAL RACES 1 AND 45 OF *PUCCINIA CORONATA AVENAE*.

F_2 geno- type	F_2 ratio	Breeding behavior in F_3	Observed	Expected	Chi- square
SSAA SSAa SSaa	4	Bred true for resistance to races 1 and 45	97	103.0	0.4
SsAA	2	Segregated for race 45 and bred true for resistance to race 1	53	51.5	0.04
SsAa Ssaa	6	Segregated for both races	164	154.5	0.6
ssAA	1	Bred true for resistance to race 1 and susceptibility to race 45	15	25.8	4.5
ssAa	2	Segregated for resistance to race 1 and bred true for susceptibility to race 45	59	51.5	1.1
ssaa	1	Bred true for susceptibility to races 1 and 45	24	25.8	0.1
Total	16		412	412.1	6.7

P for 5 degrees of freedom for chi-square of 6.7 = 0.3-0.2.

*In addition to the dominant factor S carried by Santa Fe for resistance to race 1, this variety carries either A or B (referred to as A in this analysis) in common with the dominant complementary factors of Clinton for resistance to race 1 so that the observed segregation is on a two-factor basis.

(Victoria and Bond types) occurred in the frequency of 57 to 7 completely susceptible. In F_3 with extensive studies in the greenhouse it was evident that three factors contributed toward resistance. Two (A and B) were carried by Mindo and Bond and a third (V) was carried by Victoria and Tama. A factorial analysis and the breeding behavior of seedling lines in F_3 of the cross of Mindo x Tama to race 1 are given in table 6. Seven breeding classes were established: (1) true breeding for Bond type of resistance, (2) segregation for Bond type resistance and susceptibility, (3) segregation for Bond and Victoria type of resistance, (4) segregation for both types of resistance and susceptibility, (5) true breeding for Victoria type of resistance, (6) segregation for Victoria type of resistance and susceptibility, and (7) true breeding for susceptibility. Factorial analysis presented in table 6 assumes that A and B are complementary and V is expressed only

TABLE 6. FACTORIAL ANALYSIS* AND BREEDING BEHAVIOR OF SEEDLING LINES IN F_3 OF MINDO X TAMA TO RACE 1 OF *PUCCINIA CORONATA AVENAE* ON THE BASIS OF A THREE-FACTOR DIFFERENCE.

F_2 genotype	Ratio	Breeding behavior in F_3	Expected number	Observed number	Chi-square
AABBVV AABBVv AABBvv	4	Bred true for Bond type resistance	23.4	12	5.6
AABbvv AaBBvv AaBbvv	8	Segregated for Bond type resistance and susceptibility	46.9	53	0.8
AABbVV AaBBVV AaBbVV	8	Segregated for Bond type resistance and Victoria type resistance	46.9	49	0.1
AABbVv AaBBVv AaBbVv	16	Segregated for all classes	93.8	106	0.2
AAbbVV AabbVV aaBBVV aaBbVV aabbVV	7	Bred true for Victoria type resistance	41.0	34	1.2
AAbbVv AabbVv aaBBVv aaBbVv aabbVv	14	Segregated for Victoria type resistance and susceptibility	82.0	76	0.4
AAbbvv Aabbvv aaBBvv aaBbvv aabbvv	7	Bred true for susceptibility	41.0	45	0.4
Total	64		375.0	375	8.7

P for 6 degrees of freedom for chi-square $8.7 = 0.2-0.1$.

*A and B are complementary factors for the Bond type of resistance carried by Mindo. Factor V is a simple dominant for resistance of the Victoria type carried by Tama. V is not expressed when in the presence of the factorial base which results in the Bond type of resistance, i.e., the Victoria type reaction is expressed only in susceptible germ plasm.

when in presence of germ plasm susceptible to *P. coronata avenae*. That is, when A and B are present to give the Bond type of resistance the fungus is prevented from developing to the sporulation stage, when tissue collapse (conditioned by V) normally begins.

The expected frequency for the seven breeding classes in F_3 was 4:8:8:16:7:14:7. Actual observed frequencies compared with expected on the three-factor hypothesis

did not deviate significantly. A P value of between 0.2 and 0.1 was obtained.

The epistatic effect of the Bond factors on the hypersensitive Victoria gene for resistance to crown rust was substantiated by action of race 45 on plants which gave the Bond type reaction in certain classes. As expected, all plants in the class segregating for resistance of the Bond and Victoria type with respect to race 1, when inoculated with race 45 to which the Bond type plants are susceptible, gave a characteristic Victoria type reaction.

Similarly, among 12 F_3 lines classified as breeding true for the Bond type of resistance to race 1 when further inoculated with race 45 to determine their genotype for factor V, 2 bred true for the Bond type as indicated by complete susceptibility to race 45, 7 segregated for Victoria type resistance and complete susceptibility to race 45, while 3 bred true for Victoria type of resistance. Testing the observed numbers with the expected on a single factor hypothesis a P value of between 0.8 and 0.7 was obtained.

It is evident from observations made on plants carrying both Bond and Victoria factors for resistance that the Victoria factor V for resistance to races 1 and 45 of *P. coronata avenae* is one of extreme susceptibility or hypersensitivity. Only in germ plasm of susceptible progenies can V express itself. If the fungus is allowed to develop to the sporulating stage, the host tissues can be properly acted upon by the infecting *P. coronata avenae* organism. If development of the parasitic organism is inhibited, the characteristic Victoria type of reaction will not appear. As will be brought out later, the relationship of the hypersensitive type of crown rust reaction of Victoria to susceptibility to *Helminthosporium victoriae* may be due to the release by the pathogen of a toxic material into the host cells which possess Victoria germ plasm for crown rust resistance.

INHERITANCE OF REACTION TO *HELMINTHOSPORIUM VICTORIAE*

Seedling and mature plant resistance and susceptibility to *H. victoriae* were investigated in F_2 and F_3 of six crosses—Mindó x Tama, Bond x Victoria, Mindó x Landhafer, D67 x Bond, Sac x Hajira-Joanette, and Santa Fe x Clinton. Although occasional *H. victoriae*-susceptible plants occurred in progenies of Mindó x Landhafer, two

TABLE 7. INHERITANCE OF RESISTANCE TO *HELMINTHOSPORIUM VICTORIAE* IN FIELD AND GREENHOUSE TESTS.

Crosses and location of epiphytotic	Generation	Observed or expected	No. of plants or lines			Chi-square	P
			Res.	Seg.	Susc.		
Bond x Victoria							
Greenhouse	F ₂	O E(1:3)	32 28.5		82 85.5	0.6	0.5-0.4
Mindo x Tama							
Field *	F ₂	O E(1:3)	15 17.5		55 52.5	0.5	0.5-0.4
Field *	F ₃	O E(1:2:1)	82 93.5	183 187	109 93.5	4.1	0.2-0.1

*Also checked in greenhouse.

resistant parents, it was assumed that these were the result of natural crossing with plants genetically susceptible to *H. victoriae*. Morey (25) has shown that natural crossing may be relatively high in Iowa. At two locations in 1945, he found Mindo growing adjacent to a black-glumed variety, resulted in an average of 2.91 percent natural crossing. With progeny of an interspecific cross such as Mindo x Landhafer, even more natural crossing might be expected, since flowers of some plant lines were observed to remain open for an unusually long period of time.

Segregation for resistance and susceptibility to *H. victoriae* was observed in F₂ and F₃ of crosses of Bond x Victoria and Mindo x Tama. Tama and Victoria were highly susceptible while Mindo and Bond were highly resistant to this pathogen. F₂ and F₃ data for these two crosses are given in table 7. A very good fit for a single factor difference with dominance of susceptibility was obtained in field and greenhouse tests, P values falling between 0.5 and 0.1.

As was shown in a separate part of this study, a substance is produced by *H. victoriae* which is extremely toxic to plants carrying the V factor for hypersensitivity to races 1 and 45 of *P. coronata avenae*. Evidence has been presented which indicates that the same gene governs susceptibility to *H. victoriae* and the hypersensitive type of resistance to certain races of *P. coronata avenae*, i. e., it has a pleiotropic effect. *Helminthosporium victoriae* grows as a facultative parasite which can completely destroy the



Fig. 3. Two dwarf segregates from Mindo $\times$ Landhafer. Note excessive tillering and small size in contrast to the normal plant of the same age.

host by the toxic substance produced, whereas *P. coronata avenae* is an obligate parasite which gives protection to the host by destroying host cells in the immediate vicinity of infection as fructification begins.

INHERITANCE OF CHARACTERS OTHER THAN DISEASE REACTION

DWARFNESS

Inheritance of dwarfness was extensively studied in F_2 and F_3 generations of Mindo x Landhafer, Mindo x Tama, and D67 x Bond. In one of 486 F_3 lines of Sac x Hajira-Joanette, segregation was observed for dwarfness. Dwarf plants in this population never developed beyond the grassy-tuft stage, and they occurred in the frequency of about 1 to 3. The field count was 23 normal to 9 dwarf plants compared with the expected of 24 to 8, respectively, if dwarfness is expressed as a simple recessive.

Dwarf plants which occurred in Mindo x Landhafer rarely grew more than 4 inches in height (fig. 3). Many failed to develop beyond the primary-leaf stage while those which lived beyond the two- or three-leaf stage produced an extensive tuft of leaves or short culms. Occasionally a spikelet appeared in the greenhouse which might have produced seeds had plants not been overcrowded in the pots.

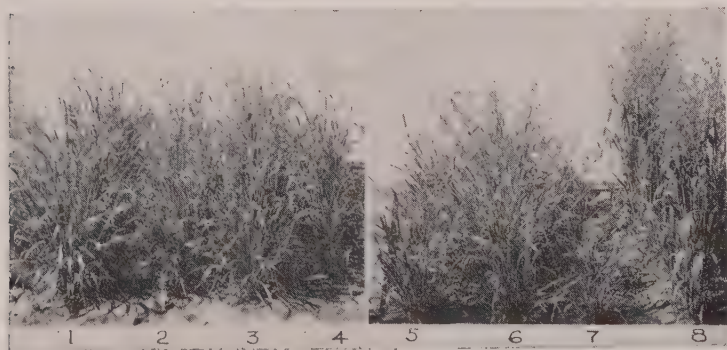


Fig. 4. True breeding F_3 dwarf lines, resulting from the cross of (1, 2, 3, 4) D67 x Bond and (5, 6, 7) Mindo x Tama. A normal row of (8) Mindo is included for comparison. Note extensive tillering of the dwarf types.

TABLE 8. INHERITANCE OF DWARFNESS IN MINDO X LANDHAFER, MINDO X TAMA AND D67 X BOND.

Crosses and location of test	Genera-tion	Observed or expected	No. of plants or lines			Chi-square	P
			Normal	Seg.	Dwarf		
Mindo x Landhafer							
Greenhouse	F ₂	O E(3:1)	122 132.8		55 44.3	3.6	0.1-0.05
Greenhouse	F ₂	O E(3:1)	238 240		82 50	0.1	0.8-0.7
Field	F ₃	O E(1:2:0)*	131 116.3	218 232.7	0 0	2.8	0.1-0.05
Mindo x Tama							
Field	F ₂	O E(15:1)	431 435.9		34 29.1	0.9	0.4-0.3
Field	F ₃	O E(7:8:1)	176 166.3	188 190	16 23.8	3.1	0.3-0.2
D67 x Bond							
Field	F ₂	O E(15:1)	439 441.6		32 29.4	0.2	0.7-0.6
Field	F ₃	O E(7:8:1)	197 192.1	224 219.5	18 27.4	3.5	0.2-0.1

*Dwarf plants in the F₂ produced no seed, therefore the expected number in the true breeding class for dwarfness would be zero.

Dwarf plants from Mindo x Tama and D67 x Bond were distinctly different from those found in Mindo x Landhafer. They ranged from about 10 to 18 inches in height when grown in pure stands in the field, produced variable amounts of seed, and tillered profusely. Photographs of some true breeding dwarfs found in these two crosses appear in fig. 4.

Table 8 gives modes of inheritance and tests for goodness of fit for dwarfness based on the breeding behavior in F₃. A good fit to expected ratios was obtained for all groups studied. Dwarfness in Mindo x Landhafer appeared to be monogenic in inheritance while dwarfness in Mindo x Tama and D67 x Bond was found to be digenic with normalness being completely dominant.

NODAL PUBESCENCE

Presence or absence of nodal pubescence was studied in F₂ and F₃ progenies of Santa Fe x Clinton, D67 x Bond, and Mindo x Landhafer. Santa Fe, Landhafer and Bond

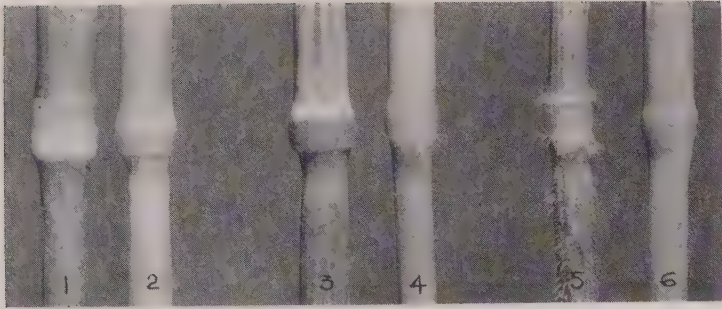


Fig. 5. Nodes of (1) Mindo, (2) Landhafer, (3) D67, (4) Bond, (5) Santa Fe and (6) Clinton showing differences in node pubescence.

have pubescent nodes while Clinton, D67 and Mindo do not (fig. 5). Only two classes were employed for classifying progenies of these crosses: pubescent and nonpubescent. No difficulty was encountered in determining this character either in the field or greenhouse, although minor differences did occur in extensiveness of pubescence. A summary of results is given in table 9 for the separate crosses. None of the three crosses had wide deviations from the expected single factor difference with pubescence incompletely dominant.

TABLE 9. INHERITANCE OF NODAL PUBESCENCE OF F_2 PLANTS AND F_3 LINES IN SANTA FE x CLINTON, D67 x BOND AND MINDO x LANDHAFER.

Crosses and location of test	Generation	Observed or expected	No. of plants or lines			Chi-square	P
			Pubescent	Segregating	Non-pubescent		
Santa Fe x Clinton Greenhouse	F_2	O E(3:1)	211 214.5		75 71.5	0.2	0.7-0.6
Field	F_3	O E(1:2:1)	96 193	219 206	97 103	1.7	0.5-0.4
D67 x Bond Greenhouse	F_2	O E(3:1)	236 247.5		94 82.5	2.1	0.2-0.1
Field	F_3	O E(1:2:1)	96 109.8	232 219.5	111 109.8	2.5	0.4-0.3
Mindo x Landhafer Greenhouse	F_2	O E(3:1)	178 199.5		76 63.5	3.3	0.1-0.05
Field	F_3	O E(1:2:1)	71 86.8	183 173.5	93 86.8	3.8	0.2-0.1



Fig. 6. Lower florets of (1) D67, (2) Bond, (3) Mindo and (4) Landhafer showing differences in number of basal hairs.

BASAL HAIRS

Threshed samples of F_3 lines and parents of Mindo x Landhafer and D67 x Bond were studied for basal hair number of the lower floret. Bond and Landhafer parents have numerous basal hairs (about 30 or more) while only a very occasional seed of D67 and Mindo has up to a

TABLE 10. INHERITANCE OF BASAL HAIR NUMBER IN F_3 LINES OF MINDO X LANDHAFER AND D67 X BOND.

Crosses	Observed or expected	No. of lines			Chi- square	P
		Basal hairs numerous	Segre- gating	Basal hairs absent		
D67 x Bond	O	109	224	106	0.2	0.9-0.8
	E(1:2:1)	109.8	219.5	109.8		
Mindo x Landhafer	O	80	184	83	1.3	0.6-0.5
	E(1:2:1)	86.8	173.5	86.8		

few hairs on the base (fig. 6). For the purpose of classifying seed for basal hairs from F_3 plant lines, basal hair numbers were classified either as numerous, absent, or segregating. Although length differences did occur in some progenies, these were not studied. The data for the two crosses and chi-square tests for goodness of fit to a 1:2:1 ratio are given in table 10. Very good agreement between observed and calculated ratios was obtained.

EARLINESS

Inheritance of earliness was investigated in two crosses, but only the results of one will be reported. In Mindo x Landhafer, lateness was confounded with dwarfness and as a consequence many plants could not be correctly classified. F_2 and F_3 progenies of Santa Fe x Clinton could be readily separated into two distinct classes for growth habit, plants heading and maturing early, like the Clinton variety, or late like the Santa Fe variety (fig. 7). Clinton has an erect seedling growth habit and, following emergence under Iowa's climatic conditions, the plants



Fig. 7. Nursery rows of (1) Clinton, (2) Santa Fe, (3) Landhafer and (4) Mindo. Note earliness of Clinton and Mindo parents and lateness of Santa Fe and Landhafer.

TABLE 11. INHERITANCE OF EARLINESS IN F_2 PLANTS AND F_3 LINES IN SANTA FE X CLINTON.

Location	Gener- ation	Observed or expected	No. of plants or lines			Chi- square	P
			Early	Segre- gating	Late		
Greenhouse	F_2	O	228		72	0.1	0.8-0.7
		E(3:1)	223.5		74.5		
Field	F_2	O	345		128	1.1	0.2-0.1
		E(3:1)	354.8		118.3		
Field	F_3	O	119	193	100	3.4	0.4-0.3
		E(1:2:1)	103	206	103		

pass in a continuous fashion through the various growth phases of jointing, heading and flowering to an early maturity. Santa Fe, on the other hand, does not uniformly pass through the different stages of plant development in rapid succession under existing climatic conditions at Ames, and the result is late maturity. After emergence plants remain for a considerable length of time in a nearly decumbent condition, and during this time tillering may be extensive. Finally, after the plants responding similarly to those of Clinton have headed, those which possess this delayed jointing character of Santa Fe begin to pass through the different stages of jointing, heading and flowering. The time difference in maturity between those responding like Santa Fe and Clinton was about one month, or even more. Similar results were obtained under both greenhouse and field conditions.

As shown in table 11, about three-fourths of the Santa Fe x Clinton plants were as early as Clinton, the early parent, and one-fourth as late as the Santa Fe parent. The field distribution, as verified by the F_3 segregation of 412 lines was in the ratio of 1 early, 2 segregating and 1 late, suggesting that one factor pair with earliness dominant governs inheritance for earliness in this cross. Very good agreements to the number expected on a single factor difference were obtained for the three groups studied. P values were between 0.8 and 0.1.

RELATIONS BETWEEN CHARACTERS

Independence or association of factors governing reaction to races 2 and 8 of *P. graminis avenae* and races 1 and 45 of *P. coronata avenae* and to *H. victoriae* with each other, and with certain seed and plant characters was

determined for five different crosses. The chi-square and P values obtained for each comparison of characters are given in table 12, as are estimated linkage intensities between characters found to be linked.

Complete association of susceptibility to *H. victoriae* and resistance to crown rust of the hypersensitive type occurred in crosses where these characters could be studied. Hypersensitive type of crown rust reaction was linked with susceptibility to *H. victoriae* in all of the thousands of plants tested. Resistance to crown rust of the hypersensitive type possessed by Victoria always was associated with susceptibility to *H. victoriae* and is apparently dependent upon the gene for susceptibility to this pathogen for its expression. In *H. victoriae*-susceptible germ plasm, resistance to crown rust can be expressed, while in its absence plants are susceptible unless there are other factors present for resistance which inhibit regular development of *P. coronata avenae*. The genetic results and interpretation agree with results obtained in a separate study where an attempt was made to determine the nature of resistance and susceptibility of the host to these two pathogens. Substances produced by the two parasites apparently have similar effects on host cells which possess the gene for susceptibility to *H. victoriae*. The difference in reaction is dependent upon the nature of the organism parasitizing the host.

Stem rust reaction and nodal pubescence were strongly linked in the repulsion phase in three crosses in which these contrasting characters were studied. Linkage intensities of $0.193 \pm .046$, $0.379 \pm .042$ and $0.387 \pm .045$ were obtained for D67 x Bond, Santa Fe x Clinton and Mindo x Landhafer, respectively. Except for the association of the hypersensitive type of resistance to crown rust and susceptibility to *H. victoriae* reported by Murphy and Meehan (28) this is the only report of linkage in oats of factors governing disease resistance with another character.

A possible linkage of reaction to stem rust and crown rust in the cross of Sac x Hajira-Joanette is suggested by the relatively high chi-square value of 22.92 ($P = < 0.01$). Because of the nature of the cross and the difficulty of studying the effects of individual factors for stem rust reaction, it could not be determined how the factors were associated. If this is a valid association, the linkage probably would involve the factors from the Hajira x Joanette

TABLE 12. CHI-SQUARE TESTS FOR INDEPENDENCE OF FACTORS GOVERNING REACTION TO *PUCCINIA GRAMINIS AVENAE*, *P. CORONATA AVENAE*, AND *HELMINTHOSPORIUM VICTORIAE* AND OTHER CHARACTERS IN FIVE OAT CROSSES.

Characters compared in different crosses	Chi-square	D. F.	P	Association of characters
Santa Fe x Clinton				
Crown rust 45 and stem rust reaction	5.5	4	0.3-0.2	Independent
Crown rust 45 reaction and earliness	7.1	4	0.2-0.1	Independent
Crown rust 45 reaction and nodal pubescence	7.6	4	0.2-0.1	Independent
Crown rust 1 and stem rust reaction	3.2	4	0.6-0.5	Independent
Crown rust 1 and earliness	2.9	4	0.6-0.5	Independent
Crown rust 1 reaction and nodal pubescence	9.9	4	< 0.05	Prob. Ind.
Stem rust reaction and earliness	6.5	4	0.2-0.1	Independent
Stem rust reaction and nodal pubescence*	112.2	4	< 0.01	Linked
Earliness and nodal pubescence	3.7	4	0.5-0.4	Independent
Sac x Hajira-Joanette				
Crown rust 1 and stem rust reaction	22.9	4	< 0.01	Poss. Linked
Mindo x Tama				
Crown rust 45 and stem rust reaction	3.7	4	0.5-0.4	Independent
Crown rust 45 and <i>H. victoriae</i> reaction	748.0	4	< 0.01	Linked or same factor
Crown rust 45 and dwarfness	0.5	4	1.0-0.9	Independent
Crown rust 1 and stem rust reaction	6.8	4	0.2-0.1	Independent
Crown rust 1 and <i>H. victoriae</i> reaction	476.9	4	< 0.01	Linked or same factor
Crown rust 1 and dwarfness	2.8	4	0.6-0.5	Independent
Stem rust and <i>H. victoriae</i> reaction	3.7	4	0.5-0.4	Independent
Stem rust reaction and dwarfness	6.4	4	0.2-0.1	Independent
<i>H. victoriae</i> reaction and dwarfness	0.5	4	1.0-0.9	Independent

TABLE 12 (Continued)

Characters compared in different crosses	Chi-square	D. F.	P	Association of characters
Mindo x Landhafer				
Crown rust 45 and stem rust reaction	2.0	4	0.8-0.7	Independent
Crown rust 45 reaction and dwarfness	7.6	2	<0.05	Prob. Ind.
Crown rust 45 reaction and basal hairs	8.5	4	0.1-0.05	Independent
Crown rust 45 reaction and nodal pubescence	1.6	4	0.9-0.8	Independent
Crown rust 1 and stem rust reaction	6.7	4	0.2-0.1	Independent
Crown rust 1 reaction and dwarfness	4.4	2	0.2-0.1	Independent
Crown rust 1 reaction and basal hairs	4.6	4	0.4-0.3	Independent
Crown rust 1 reaction and nodal pubescence	6.3	4	0.2-0.1	Independent
Stem rust reaction and dwarfness	2.5	2	0.3-0.2	Independent
Stem rust reaction and basal hairs	6.5	4	0.2-0.1	Independent
Stem rust reaction and nodal pubescence*	54.4	4	<0.01	Linked
Dwarfness and basal hairs	3.6	2	0.2-0.1	Independent
Dwarfness and nodal pubescence	7.1	2	<0.05	Prob. Ind.
Basal hairs and nodal pubescence	5.2	4	0.3-0.2	Independent
D67 x Bond				
Crown rust 1 and stem rust reaction	16.6	4	<0.01	Prob. Ind.
Crown rust 1 and dwarfness	9.0	4	0.1-0.05	Independent
Crown rust 1 and basal hairs	2.7	4	0.7-0.6	Independent
Crown rust 1 and nodal pubescence	11.7	4	<0.02	Prob. Ind.
Stem rust reaction and dwarfness	3.7	4	0.5-0.4	Independent
Stem rust reaction and basal hairs	1.4	4	0.9-0.8	Independent
Stem rust reaction and nodal pubescence*	231.0	4	<0.01	Linked
Dwarfness and basal hairs	12.5	4	<0.02	Prob. Ind.
Dwarfness and nodal pubescence	7.5	4	0.2-0.1	Independent
Basal hairs and nodal pubescence	2.8	4	0.7-0.6	Independent

* Linkage intensities between factors for stem rust reaction and nodal pubescence in D67 x Bond, Santa Fe x Clinton and Mindo x Landhafer were determined to be $0.193 \pm .046$, $0.379 \pm .042$ and $0.387 \pm .045$, respectively.

parent, since the factor for resistance to stem rust from Sac is probably similar to that of Clinton and Mindo which was independently inherited.

All other character combinations listed in table 12 probably were inherited independently. In individual cases where P values of below .05 were obtained, a close study of the data revealed that the high chi-square values could be attributed to deviations from the expected through a non-random sample. Comparisons with other characters in the same and other crosses also substantiated the conclusions that these characters probably were inherited independently.

DISCUSSION OF RESULTS

Studies on inheritance of reaction to *Puccinia graminis avenae* indicate that resistance and susceptibility to races 2 and 8 in seedling and mature plant stages are dependent on a single factor pair in crosses of Mindo x Landhafer, Mindo x Tama, Santa Fe x Clinton and D67 x Bond and on three factor pairs in the cross of Sac x Hajira-Joanette.

Mindo, D67, Clinton and probably Sac each possess a single dominant gene which governs resistance to the two races. The factor of Tama for resistance to race 2 is different from the one of Mindo and similar varieties which gives resistance to races 2 and 8. In progenies of Mindo x Tama no plants were obtained which were susceptible to race 2, while segregation was observed for reaction to race 8 or a composite of the two races on a monohybrid basis. When a composite of the two races was used, plants classified as susceptible actually were mesothetic when more closely examined, while if race 8 was used as inoculum only a susceptible type reaction was observed. These observed segregations for a single dominant factor pair for reaction to stem rust are in accord with those of Garber (12, 13), Griffiee (17), Hayes, et. al. (18), Dietz (7), Waterhouse (42), Welsh (44), Smith (35), Hayes, et al. (19), Torrie (40), Cochran, et al. (3), and Ko, et al. (21). The existence of an allelomorphic series of factors for resistance to stem rust, as was observed in the Mindo x Tama cross, was also reported by Smith (36).

Stem rust reaction as observed in the crosses Santa Fe x Clinton, Mindo x Landhafer and D67 x Bond was found strongly linked in the repulsion phase with nodal pu-

bescence. Such an association previously has not been reported. This relationship can be a visual aid to the breeder in selecting stem rust resistant progeny in hybrid populations.

Inheritance of stem rust reaction was more complex in the Sac x Hajira-Joanette cross. Segregation was somewhat similar to that observed in Mindo x Tama except that segregation was for three factor pairs instead of one. Plants having a mesothetic reaction to a composite inoculum of races 2 and 8 in the seedling stage appeared in F_2 in the ratio of 1 to 63. Plants having the mesothetic reaction to the composite inoculum bred true in the next generation, while resistant plants either bred true or segregated for resistance and the mesothetic type reaction.

When inoculated with race 2 all progenies were resistant (types 1 and 2), while with race 8 only those responding mesothetically to the composite of the two races gave a susceptible reaction. Analyzing such an observed segregation, four factors governing stem rust reaction must be involved in the cross even though segregation occurred for only three factor pairs. One factor pair would behave similarly to that described in the cross of Mindo x Tama, i. e., Sac would carry a factor for resistance to races 2 and 8, while an allele for resistance to race 2 would be carried by Hajira x Joanette. Segregation thus would occur at this locus for resistance to race 8 or a composite of the two races, while no segregation could be observed for reaction to race 2, since all progeny would give a resistant reaction. The other two factors which contribute resistance to race 8 would be carried by Hajira x Joanette as dominants. When these factors from Hajira x Joanette are combined with the one from Sac, segregation on a three-factor difference would result when tested against race 8 or a composite collection of races 2 and 8. Such an analysis would not conflict with Welsh (46) who has intensively studied inheritance of stem rust in Hajira and Joanette varieties and hybrids of the two varieties.

A possible linkage may exist between the factors for stem rust resistance possessed by Hajira x Joanette with reaction to race 1 of crown rust. However, since the relationship between the factors for stem rust and crown rust reaction cannot be truly evaluated, further work will be necessary to determine the validity of this linkage.

Five independently inherited factors (A, B, L, S and V) were found to govern resistance to races 1 and 45 of

P. coronata avenae in this investigation. Only factors A, B and V previously have been reported. Factors A and B were inherited as dominant complementary factors for resistance to race 1 in five of six crosses studied. These factors are responsible for the Bond type of resistance (type 0, nearly immune) to race 1. Hayes, et al. (19), Weetman (44), Cochran, et al. (3) and Ko, et al. (21) similarly reported the complementary action of A and B factors possessed by Bond for resistance to certain races of *P. coronata avenae*.

Hypersensitive type of resistance to races 1 and 45 possessed by Victoria and Tama was inherited as a simple dominant. This is in agreement with inheritance studies of Weetman (44), Cochran, et al. (3) and Murphy and Meehan (28). A complete linkage of the V factor for reaction to *P. coronata avenae* with susceptibility to *Helminthosporium victoriae* was observed in these studies. Since susceptibility to *H. victoriae* and resistance to races 1 and 45 of *P. coronata avenae* appear to be dependent upon cellular sensitiveness of the host to toxic substances produced by these two fungi, the single V factor is considered pleiotropic in its effects and is responsible for resistance and susceptibility to both diseases. With an obligate parasite such as *P. coronata avenae* host resistance would result because of the physical barrier created by severing the food supply by collapse of cells surrounding the point of infection. Conversely, complete susceptibility would result with *H. victoriae*, a facultative parasite, which can continue to parasitize the plant until the susceptible host is completely destroyed by diffusion of a toxic substance into the host cells. Since *H. victoriae* is prevalent in the major part of the oat production area of the eastern half of the United States it would appear inadvisable at this time to continue using the V factor for resistance to race 45 in subsequent breeding efforts.

The L and S factors for resistance to crown rust of Landhafer and Santa Fe, respectively, govern resistance to races 1 and 45 as simple dominants in both seedling and mature plant stages. With Landhafer, however, expression of the L factor becomes less effective in controlling crown rust as plant tissues become older, and some infection and sporulation does occur. This was evident both in the greenhouse and field. These two factors, especially the one (S) from Santa Fe, are excellent sources for resistance to race 45. Factors A and B will not control resistance to race 45

which parasitizes such varieties as Bond, Clinton, Benton, Sac, Mindo and Bonda.

No disease, plant or seed character was found linked with the factors for crown rust resistance. All were inherited independently. This is in accord with findings of Smith (36), Hayes, et al. (19) and Torrie (40).

Dwarfness was variously inherited in crosses of normal varieties. Segregation for dwarfness occurred as a simple recessive in Mindo x Landhafer and as a double recessive in Mindo x Tama and D67 x Bond. Dwarf plants occurred in an F_3 line of Sac x Hajira-Joanette in the ratio of about one to three or as a simple recessive. Dwarfness in this latter case probably resulted from a mutation, since it was the only line out of 486 grown which segregated for this character. Dwarf segregates of the double recessive type were about one-half normal for height, tillered profusely and generally produced seed, while those segregating as a simple recessive died. These latter types did not develop beyond the seedling stage. The dwarf character which is not lethal might be usable in the development of a type for grazing purposes. Dwarfness was not observed to be linked with any of the characters with which it was compared.

In the cross of Santa Fe x Clinton earliness was simply inherited, although varying degrees of complexity have been previously reported for this character. A single dominant determined earliness. No difficulty was encountered in the separation of plants into two distinct types for growth habit. Earliness was inherited independently of reaction to stem rust, crown rust and nodal pubescence. Partial dominance of earliness has been reported by Noll (32), Garber and Quisenberry (14), Shaw and Bose (35), and Torrie (40).

Basal hair number in two *Avena sativa* x *A. byzantina* crosses (Mindo x Landhafer and D67 x Bond) was monogenic in inheritance as was reported by Fraser (11), Smith (36), Shaw and Bose (35), Hayes, et al. (19), and Torrie (40). The factor for basal hair number was inherited independently of stem rust reaction, crown rust reaction, dwarfness and nodal pubescence. Except for association with other kernel characters such as spikelet disarticulation, hairy rachilla, floret disjunction and awning, basal hairs have been reported by various workers as inherited independent of other characters studied.

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